AMERICAN MUSEUM NOVITATES

Published by
Number 1343 THE AMERICAN MUSEUM OF NATURAL HISTORY April 11, 1947
New York City

VARIATION OF TWO CHARACTERS IN *BUFO FOWLERI* AND *BUFO AMERICANUS*

BY ALBERT P. BLAIR[1]

In a previous paper (Blair, 1941) it was shown that early-breeding toads at Bloomington, Indiana, have relatively large hind leg warts and narrow interparotoid spaces as compared with late-breeding toads at the same locality, that the change in size of hind leg warts and interparotoid spaces is gradual, and that the early-breeding and late-breeding populations are referable to what is generally considered *Bufo americanus* and *B. fowleri*, respectively. The present paper will be concerned with three seasonal population samples from Oradell, New Jersey, and with individual collections of *B. americanus* and *B. fowleri* from the following localities: Elizabeth Islands, Massachusetts; Wilburton, Oklahoma; Oshkosh, Wisconsin; Polk, Pennsylvania; Utica, New York; Bronx, New York; Leonia, New Jersey; Englewood, New Jersey. Only Fowler's toad occurs on the Elizabeth Islands. At Polk, Oshkosh, and possibly Utica the American toad is the only form. Both the American toad and Fowler's toad occur at Wilburton, Leonia, Englewood, and probably the Bronx. The collection from Wilburton consists of two population samples, each relatively homogeneous, made on different dates, and referable to the two species under consideration. The Bronx, Englewood, and Leonia collections are referable to *B. americanus*. All specimens here considered are adult males.

At Bloomington it was found that by the second week in May the breeding population was relatively homogeneous and referable to *Bufo fowleri*. At Oradell none of the three collections was homogeneous. The May 19 sample was predominantly *americanus*-like, while *B. fowleri* characteristics predominated in the June 13 and June 28 samples. But even the June 28 sample was by no means as homogeneous as the Bloomington sample of May 7, 1940.

Let us examine the Oradell toads with respect to the two characters under consideration (tables 1 and 2). The average hind leg wart size for Oradell toads for May 19 is 2.00 mm., a figure intermediate between the Bloomington averages for April 29 and April 30, at which time the transition from *americanus* to *fowleri* is marked in the Bloomington population. By June 13 the Oradell average drops to 1.65 mm. It is to be noted that the Oradell average changes less in 25 days than the Bloomington average changes from one night to the next. But by June 28 the Oradell average is significantly lower than the May 7 Bloomington average, despite the fact that in general Oradell toads of June 28 are more heterogeneous than Bloomington toads of May 7.

The situation with respect to interparotoid space is quite different. The interparotoid space mean for May 19 Oradell toads does not differ significantly from that of May 7 Bloomington toads, although the May 7 Bloomington population is predominantly *fowleri*-like, while the May 19 Oradell population is predominantly *americanus*-like. No increase of interparotoid space is evident in subsequent collections; in fact, the June 13 and June 28 samples show smaller interparotoid spaces than the first sample.

Both Elizabeth Islands and Wilburton *fowleri* are quite similar to May 7 Bloomington and June 28 Oradell toads (*Bufo fowleri*) with respect to hind leg wart size; only Elizabeth Islands and June 28 Oradell toads differ significantly. But with respect to interparotoid space, Elizabeth Islands

[1] Department of Animal Behavior.

toads differ significantly from May 7 Bloomington and June 28 Oradell toads, and, in fact, from all other samples. No data are available for interparotoid space of Wilburton *fowleri*.

Among the American toad samples from localities other than Oradell and Bloomington, the largest hind leg warts are found at Polk and Utica; in both localities hind leg warts are much larger than in the earliest Bloomington sample, which is presumably most *americanus*-like. Means for Polk and Utica differ significantly.

The smallest hind leg warts are found in the Wilburton sample; the mean is significantly smaller than the earliest Bloomington mean. Hind leg wart means of approximately equal magnitude are found in the samples from Oshkosh, Bronx, Leonia, and Englewood; these means are comparable with the mean for the earliest Bloomington sample.

The pattern of variation of interparotoid space size in individual American toad samples does not follow that of hind leg wart size. In all samples interparotoid space is larger than in the earliest Bloomington sample; the difference, however, is not significant with respect to Oshkosh and Wilburton samples. The adjacent Leonia and Englewood samples do not differ significantly, nor do they differ from any of the three samples from nearby Oradell. The Englewood sample does not differ significantly from the Bronx sample; however, the Leonia sample does. The Bronx and Utica samples do not differ significantly.

Certain conclusions may be drawn. In general, adjacent populations tend to resemble one another more closely than they do distant populations. Different characters vary independently. Hybridization presumably has taken place both at Bloomington and Oradell. The temporal ranges of variation, however, are different at these two localities. To what extent such differences are attributable to the extent of hybridization and to what extent to geographical variation is not completely apparent. It is the belief of the writer that hybridization has progressed further at Oradell.

Ultimately, adequate interpretation of such variation data must depend upon reso-

TABLE 1

MEANS AND STANDARD DEVIATIONS OF THE MEANS FOR HIND LEG WART AND INTERPAROTOID SPACE (MEASUREMENT IN MILLIMETERS)

		Hind Leg Wart		Interparotoid Space	
		N	Mean ± σm	N	Mean ± σm
Bloomington	April 15, 1940	158	m = 2.57 ± 0.04	158	m = 7.85 ± 0.08
	April 29, 1940	243	m = 2.33 ± 0.03	62	m = 8.46 ± 0.12
	April 30, 1940	75	m = 1.56 ± 0.07	17	m = 8.40 ± 0.25
	May 5, 1940	58	m = 1.76 ± 0.09		
	May 6, 1940	117	m = 1.75 ± 0.07		
	May 7, 1940	138	m = 1.34 ± 0.04	34	m = 9.51 ± 0.14
	May 7, 1939			162	m = 9.66 ± 0.11
Oradell	May 19, 1946	33	m = 2.00 ± 0.13	33	m = 9.45 ± 0.21
	June 13, 1946	40	m = 1.65 ± 0.09	40	m = 9.05 ± 0.15
	June 28, 1946	20	m = 1.18 ± 0.08	20	m = 9.07 ± 0.20
fowleri	Elizabeth Islands	13	m = 1.46 ± 0.08	13	m = 11.16 ± 0.28
	Wilburton	40	m = 1.39 ± 0.04		
americanus	Polk	43	m = 3.10 ± 0.06		
	Oshkosh	51	m = 2.37 ± 0.05	17	m = 8.29 ± 0.18
	Utica	29	m = 3.48 ± 0.10	29	m = 8.56 ± 0.11
	Bronx	36	m = 2.41 ± 0.065	36	m = 8.34 ± 0.13
	Leonia	58	m = 2.56 ± 0.065	58	m = 9.09 ± 0.12
	Englewood	17	m = 2.57 ± 0.08	17	m = 8.61 ± 0.26
	Wilburton	25	m = 2.21 ± 0.08	25	m = 8.24 ± 0.24

TABLE 2

Critical Ratios

(The critical ratio is defined as the ratio of the difference between the means to the standard error of the difference between the means; a C.R. of 2.5 or greater is taken as significant.)

	Interparotoid Space	Bloomington							Oradell			*fowleri*		*americanus*					
	Hind Leg Wart	April 15, 1940	April 29, 1940	April 30, 1940	May 5, 1940	May 6, 1940	May 7, 1940	May 7, 1939	May 19, 1946	June 13, 1946	June 28, 1946	Elizabeth Islands	Wilburton	Polk	Oshkosh	Utica	Bronx	Leonia	Englewood	Wilburton
Bloomington	April 15, 1940		4.2	2.1	—	—	10.3	13.3	7.1	7.1	5.7	11.4	—	—	2.2	5.2	3.2	8.6	2.8	1.5
	April 29, 1940	4.8		0.2	—	—	5.7	7.4	4.1	3.1	2.6	9.0	—	—	0.8	0.6	0.7	3.7	0.5	0.8
	April 30, 1940	12.5	10.0		—	—	3.9	4.6	3.2	2.2	2.1	7.3	—	—	0.3	0.6	0.2	2.5	0.6	0.5
	May 5, 1940	8.2	6.0	1.8		—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
	May 6, 1940	10.2	7.6	1.9	0.1		—	—	—	—	—	—	—	—	—	—	—	—	—	—
	May 7, 1940	21.7	19.8	2.7	4.3	5.1		0.8	0.2	2.2	1.8	5.3	—	—	5.4	5.2	6.1	2.3	3.1	4.6
	May 7, 1939	—	—	—	—	—	—		0.9	3.3	2.6	5.0	—	—	6.5	7.1	7.8	3.5	3.7	5.4
Oradell	May 19, 1946	4.2	2.5	3.0	1.5	1.7	4.9	—		1.5	1.3	4.9	—	—	4.2	3.7	4.5	1.5	2.5	3.8
	June 13, 1946	9.3	7.2	0.8	0.9	0.9	3.1	—	2.2		0.1	6.6	—	—	3.2	2.6	3.6	0.2	1.5	2.9
	June 28, 1946	15.5	13.5	3.6	4.8	5.3	1.8	—	5.5	3.9		6.1	—	—	2.9	2.2	3.1	0.1	1.4	2.6
fowleri	Elizabeth Islands	12.4	10.2	0.9	2.5	2.7	1.3	—	3.5	1.6	2.5		—	—	8.6	8.6	9.1	6.8	6.7	7.9
	Wilburton	21.1	18.8	2.1	3.8	4.5	0.9	—	4.5	2.6	2.4	0.8		—	—	—	—	—	—	—
americanus	Polk	7.4	11.5	16.7	12.4	14.6	24.4	—	7.6	13.4	19.2	16.4	23.7		—	—	—	—	—	—
	Oshkosh	3.1	0.7	9.4	5.9	7.2	16.1	—	2.7	7.0	12.6	9.6	15.3	9.1		1.3	0.2	3.6	1.0	0.2
	Utica	8.4	11.0	14.0	12.2	12.6	19.9	—	9.0	12.9	17.9	15.7	19.3	3.3	9.9		1.3	3.3	0.2	1.2
	Bronx	2.1	1.1	8.9	5.9	6.9	14.1	—	2.8	6.8	11.9	9.2	15.7	7.8	0.5	8.9		4.2	0.9	0.4
	Leonia	0.1	3.2	10.5	7.2	8.5	16.0	—	3.9	8.2	13.4	10.7	18.0	7.1	2.3	7.7	2.3		1.6	3.2
	Englewood	0.0	2.8	9.5	6.7	7.7	13.7	—	3.7	7.6	12.3	9.8	13.2	5.3	2.1	6.3	1.5	0.1		1.0
	Wilburton	4.0	1.4	6.1	3.7	4.3	9.7	—	1.4	4.7	9.1	6.6	9.2	9.0	1.7	9.9	2.0	3.4	3.2	

lution of two questions. First, what is the nature of genetic control of breeding time? Is the control genetically simple, determining merely that the American toad breeds within a definite temperature range and that Fowler's toad breeds within a different temperature range, with relatively early- or late-breeding toads of a given species being such only because of environmental conditions? Or is the control complex, depending on many genes, with early-breeding Fowler's toads genetically different from late-breeding Fowler's toads? And if so, are hind leg wart and interparotoid space size genes linked to genes for time of breeding?

Second, to what extent has hybridization altered the range of variation in Fowler's toad and the American toad? Wherever the two species occur together some intermediates are found (Blair, 1941). Is this exchange of genes of very recent origin or has it played an important role in the configuration of the species at least from the last glacial recession? The present range of the American toad is from northern Georgia and northeastern Texas on the south to James Bay on the north; the western edge of the range is the eastern boundary of the prairie plains. The Canadian population has been described as a separate subspecies, *B. americanus copei*, but the known specimens are so few and the differences so poorly defined that appraisal of this form is not yet possible. In the northern Great Plains the American toad is replaced by *B. hemiophrys*, an allied form whose range is entirely within glaciated territory. In the southeastern United States the American toad is replaced by the closely allied *B. terrestris;* at the line of juncture of the two forms intermediates are found.

Roughly speaking, Fowler's toad coexists with the American toad over the southern half of the range of the American toad. In the southeast it is, as is the American toad, replaced by *B. terrestris* with intermediates along the line of junction. *Bufo fowleri* does not go so far west or northwest as *B. americanus*. Along the eastern border of the prairie plains Fowler's toad is replaced, with a varying degree of intergradation, by *Bufo woodhousii*, its closest relative. West of the line of junction lies a narrow north-south strip (at places 100 miles or more wide) where *B. americanus* and *B. woodhousii* coexist; intermediates between these two forms are also present.

The writer has in the past referred to the toads of the lower Mississippi Valley as *B. fowleri*, and this is perhaps the best designation. This population has, however, some of the characteristics of the American toad.

From a number of localities (northern Michigan, northwestern Pennsylvania, upstate New York, the Great Smoky Mountains) the writer has seen collections of large, dark, excessively spiny American toads which are quite distinctive. Do such populations represent ecological segregates, or is it too much to suppose that they constitute the most homogeneous American toad stock and that most so-called American toads are more or less contaminated with genes of the *fowleri-woodhousii* group? The findings of Moore (1944) are suggestive. In an investigation of the embryonic developmental rate of toads in the vicinity of New York City, it was found that *B. fowleri* from Flushing, Long Island, New York, where the American toad does not occur, had a time interval of 107 hours between first cleavage and gill circulation. Toads from Bear Mountain, New York, where the population is "good" *americanus*, showed an interval of 91 hours. Finally, American toads from Tenafly, New Jersey, where there has presumably been considerable hybridization, showed an interval of 98 hours. This is striking confirmation, from a physiological investigation, of morphological taxonomic findings.

In summary, then, morphological characters of Fowler's toad and the American toad vary from locality to locality and from breeding date to breeding date in a given locality. It seems likely that this variability is due both to geographical variation and to hybridization.

ACKNOWLEDGMENT

Mr. C. M. Bogert of the Department of Amphibians and Reptiles made available the animals of the Utica, Bronx, Englewood, and Leonia series, aided in collection of the Oradell series, and read the manuscript. Others reading the manuscript and making suggestions were Drs. L. R. Aronson, Th. Dobzhansky, J. A. Moore, and J. A. Oliver. Dr. F. A. Beach assisted in collection of the Oradell series.

LITERATURE CITED

BLAIR, A. P.
1941. Variation, isolating mechanisms, and hybridization in certain toads. Genetics, vol. 26, pp. 398–417.

MOORE, J A.
1945. Embryonic temperature tolerance and rate of development in populations of the Bufo americanus-Bufo fowleri complex. Year Book Amer. Phil. Soc., 1944, pp. 157–158.